free or united carpels, when united the ovary superior, 3–5-loculate; styles or sessile stigmas as many as the carpels; ovules one per carpel and basal, or several to many on axile placentae, anatropous to anacampylotropous. Fruit an achene or 3–5-valved loculicidal capsule. Seeds reniform to roundish; seed-coat smooth, punctate, tuberculate, or longitudinally ridged; saccate caruncle or hilar peg present or absent. Embryo peripheral, curved; cotyledons fleshy; endosperm starchy. TYPE GENUS: *Mollugo* L.

A small family of 14 more or less weedy genera containing about 95 species distributed primarily in the tropics and subtropics of both hemispheres. The family is best developed in southern Africa, where twelve genera occur. Of these, seven are confined to Africa (*Adenogramma* Reichenb., *Coelanthum* E. Mey. ex Fenzl, *Hypertelis* E. Mey. ex Fenzl, *Pharnaceum* L., *Polpoda* Presl, *Psammotropha* Eckl. & Zeyh., *Suessenguthiella* Friedr.), three extend to southwestern Asia (*Corbichonia* Scop., *Limeum* L.) or southeastern Asia (*Gisekia* L.), and two are pantropical weeds (*Glinus* L., *Mollugo* L.). *Glischrothamnus* Pilg. is known only from Brazil, and *Macarthuria* Hueg. is restricted to Australia. *Mollugo* and *Gisekia* are each represented in our area by a single species, *Glinus* by two. *Gisekia* has only recently been found in Florida, and is thus not included in the older floristic works.

The genera included here have appeared in the literature under several family names. Bentham & Hooker considered them a tribe, Mollugineae, in their order Ficoideae (family Ficoidaceae). Baillon recognized a series Mollugineae in his family Portulacaceae. In the two editions of Engler & Prantl's *Die Natürlichen Pflanzenfamilien* they appear in the Aizoaceae, and in both Small's *Manual of the Southeastern Flora* and the *North American Flora* under Tetragoniaceae (= Aizoaceae). However, taxonomic opinion (Hutchinson, 1926, 1959; Friedrich, 1955; Takhtajan, 1959; Adamson, 1960; Eckardt, 1964; Cronquist, 1968) is now heavily in favor of segregating this group from the Aizoaceae. In this case the family name Molluginaceae Hutchinson is conserved against Glinaceae Link.

Of the four tribes now recognized in the family (Eckardt), only the Mollugineae (including *Mollugo* L., and *Glinus* L., with carpels united and several to many seeds per locule) and Gisekieae (containing only *Gisekia*, with apocarpous gynoecium and solitary, basal ovules) reach our area, while the tribes Corbichonieae (formerly Orygieae) and Limeeae are confined to the Old World.

From the related Aizoaceae the Molluginaceae differ in having a scarcely (if at all) succulent habit; in possessing red pigments of the anthocyanin rather than the betacyanin type; in lacking anomalous secondary growth in the stems and roots; in having floral parts few, usually free (except in *Coelanthium*), hypogynous, and cyclically arranged; and in lacking a calyx tube. The family is considered to be closely allied with the Phytolaccaceae through the apocarpous gynoecium of *Gisekia* and the solitary,

basal ovules of the tribe Limeeae, but differs in having cymose-dichasial, rather than racemose or spicate, inflorescences. There are also relationships with the Portulacaceae and Caryophyllaceae.

Available chromosome counts indicate that $x = 9$ for the Molluginaceae, with several levels of polyploidy represented in the common genera and species.

From a study of the floral morphology and vascular anatomy of seven species in four genera (*Gisekia*, *Glinus*, *Mollugo*, *Semonvillea* [*Limeum*]) Sharma (1963a) concluded that progressive condensation of the floral axis has resulted in a change from acyclic to cyclic origin of the tepals and tepal traces and from independent origin of the tepal and stamen traces to various stages of cohesion and adnation. In the androecium he suggests reduction from three pentamerous cycles to one (the innermost); in the gynoecium reduction from three bundles in each carpel to two in *Limeum pterocarpum* (Gay) Heimerl (as *Semonvillea pterocarpa* Gay) through the loss of the dorsal bundle; and in the placentation reduction from axile to basal (*Gisekia*) or partially parietal.

The embryology of a few genera (*Gisekia*, *Glinus*, *Limeum*, *Mollugo*, and *Corbichonia*) has been studied, although not intensively. Ovules vary from anatropous to anacampylotropous. The inner of two integuments forms the micropyle. An aril may be present around the funiculus (*Glinus*, *Corbichonia*, *Macarthuria*). A normal Polygonum-type embryo sac develops within the crassinucellar ovule, followed by either a caryophyllad or solanad type of embryogeny. Anthers are tetrasporangiate. The pollen grains are 3–5-colpate or zonicolporoidate (i.e., distributed around the equator of the grain; Sharma) and are usually 3-celled when shed.

The family is of no great significance either economically or horticulturally, but individual species may be utilized regionally as vegetables or in folk medicine or serve as grazing plants for livestock.

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## KEY TO THE GENERA OF MOLLUGINACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *low herbs with simple, alternate, opposite or falsely whorled, often distinctly unequal, exstipulate leaves; stems mostly prostrate*

*(to ascending); inflorescence an axillary or terminal, diffuse or congested cyme; flowers incomplete, small and inconspicuous, regular, hypogynous; sepals 5; petals none; stamens mostly 3–5, alternate with the sepals (or with the carpels when 3 ), free or slightly united basally in a shallow ring; carpels 3–5, free or united in a several-loculate superior ovary; ovules 1 to many; placentation basal or axile; fruit an achene or many-seeded loculicidal capsule; seeds ± reniform, the seed-coat smooth, punctate, tuberculate, or longitudinally ridged.*

A. Plants glabrous; seeds lacking caruncle and filiform appendage.
   B. Carpels 5, free; ovule 1, basal; fruit a thin-walled achene; petiole margins often decurrent on the stem, the ribs often bearing scale-like hairs. ..... 1. *Gisekia.*
   B. Carpels 3(–5), united; ovary 3(–5)-loculate; ovules numerous in each locule on axile placentae; fruit a 3(–5)-valved loculicidal capsule; petiole margins not decurrent. ..... 2. *Mollugo.*

A. Plants thinly to densely stellate-pubescent; seeds numerous, each bearing a long filiform appendage and a whitish, saccate caruncle around the persistent funiculus; sepals mucronate tipped; ovary compound, 3(–5)-loculate; stigmas 3(–5), sessile or nearly so. ..... 3. *Glinus.*

Tribe GISEKIEAE Endl.

1. **Gisekia** Linnaeus, Mant. Pl. Alt. 554, 562. 1771.

Scarcely succulent annual herbs with prostrate to ascending branches radiating from a central axis. Stems glabrous, reddish, subequal, with opposite branching; nodes swollen. Leaves exstipulate, opposite to fasciculate, the fascicles separated by distinct internodes; blades narrowly lanceolate to linear-oblong, unequal, entire, the margins sometimes revolute at maturity; midvein prominent below, depressed above, secondary veins inconspicuous; margins of the petiole or leaf-base decurrent, forming ribs on the terete stems. Inflorescence an axillary or terminal several-flowered compound dichasium [varying to umbellate]. Flowers small, perfect [or imperfect], about 2 mm. long. Sepals 5, free, boat-shaped, translucent margins whitish below, pinkish above. Stamens 5[–15], alternate with the sepals; filaments basally dilated; anther basifixed, 2-loculate at anthesis, dehiscing by lateral longitudinal slits, white. Gynoecium apocarpous, carpels 5 [3 or 10], laterally compressed, wall translucent, covered with soft, whitish papillae, at maturity the carpel margins weakly erose-winged; style short, inserted on inner side of summit of carpel, erect in bud, curving outward at maturity; stigma ± terminal; ovule solitary in each carpel, basal. Fruit a thin-walled achene. Seed nearly circular in outline, laterally compressed ± lenticular in section; seed coat black, lustrous, finely punctate at maturity. Embryo nearly annular, peripheral; cotyledons oblong, fleshy; endosperm starchy. TYPE SPECIES: *G. pharnacioides* L. (Named for Paul Dietrich Giseke, 1741–1796, professor at Hamburg, Germany.)

A small genus of perhaps five species distributed primarily in the warmer, drier parts of tropical and subtropical Africa and Asia. The most

widespread of these, *G. pharnacioides*, $2n = 36$, is the only species occurring in our area, apparently as a very recent adventive. Godfrey described and illustrated plants of this species from orange groves in Orange and Polk counties in central peninsular Florida, where they flourish, sometimes in large numbers, in loose cultivated sands. The species may be spreading from this area. This habitat is similar to that of the Indian representatives of this species (which the plants of our area closely approach) as described in detail by Joshi & Kambhoj, who rarely found the species in other than sandy habitats, with the plants appearing after the first few rain showers and the life-cycle being completed in five to eight weeks. This species, with its leaves with large, thick-walled epidermal cells bearing thick cuticle and wax layers and the palisade cell layers internal, is well adapted to xerophytic conditions. The stems, leaves, and all floral organs are conspicuously white-flecked by bundles of raphides produced in the parenchymatous tissues.

There is disagreement concerning the systematic position of the genus. It has been referred to the Phytolaccaceae (DeCandolle, Baillon, Heimerl) but was excluded from that family by Walter; to the Portulacaceae (Gagnepain), a position that has found no support from other workers; to the Ficoidaceae or Aizoaceae (Bentham & Hooker, Pax & Hoffmann); and, most recently, to the Molluginaceae (Hutchinson, Friedrich, Eckardt, Takhtajan, Cronquist). In the Aizoaceae, Molluginaceae, and Phytolaccaceae *Gisekia* comprises a monotypic tribe, Gisekieae Endl. With the Phytolaccaceae *Gisekia* shares free carpels with solitary, basal ovules. Among the genera of Molluginaceae *Gisekia* is perhaps closest (but only distantly related) to *Limeum*. In its anacampylotropous ovules with few-layered nucellar epidermal caps *Gisekia* compares favorably with other Molluginaceae, rather than Phytolaccaceae. It differs from those species of Aizoaceae so far investigated in lacking radially stretched epidermal cells in the nucellar caps and in the absence of starch grains in the embryo sac. The pollen is tricolpate and three nucleate when shed (Sharma, 1963b; Joshi & Rao). Secondary growth is normal, rather than anomalous. The floral vascular anatomy of *G. pharnacioides* has been described by Sharma (1963a). The nature of the red pigments, whether antho- or betacyanous, has not yet been determined.

Orthographic variations of the generic name include *Giesekia*, *Gieseckia*, *Giseckia*, *Gisechia*, and *Giesechia*, while the specific name may appear as "*pharnaceoides*", rather than as the original "*pharnacioides*" (Adamson).

The genus is of little economic significance. *Gisekia pharnacioides* is an important grazing plant for cows, goats, sheep, and camels in India, and is used in folk or Ayurvedic medicine against a broad range of complaints, including scabies, rhinitis, bronchitis, leprosy, leucoderma, urinary diseases, and as a powerful antihelminthic in cases of *Taenia* (tapeworm) infection. The leaves are used in the preparation of *dal* (the split seeds of various legumes), and as a potherb in times of famine (Uphof).

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Tribe MOLLUGINEAE [Fenzl]

2. **Mollugo** Linnaeus, Sp. Pl. 1: 89. 1753; Gen. Pl. ed. 5. 39. 1754.

Rather variable glabrous annual herbs [or subshrubs] of dry, open, disturbed habitats. Stems prostrate to decumbent, radiating from a short, slender, tapering taproot, dichotomously much-branched, slender, wiry, with slightly swollen nodes. Leaves simple, unequal, exstipulate [or stipules rare, obsolete or early deciduous], scarcely fleshy, forming basal and cauline whorls of 3–8, the whorls often separated by long internodes, basal leaves usually largest, up to 4 cm. long, cauline leaves gradually reduced upwards; blades linear lanceolate to oblong, elliptic, spatulate or obovate, the apex acute to obtuse, the base gradually tapering to a short, membranaceous-margined petiole. Inflorescence an axillary [or terminal] umbellate cluster of 2–5 inconspicuous, short-pedicellate flowers, the pedicels strongly reflexed after flowering. Sepals 5, free, imbricate (or quincuncial), green without, whitish within, margins hyaline, spreading at anthesis. Petals none.[2] Stamens usually 3 and alternate with the carpels, sometimes 4 or 5 [rarely more] and alternate with the sepals, united basally by a very shallow ring of filament tissue; anthers versatile, the 2 lobes separated below. Carpels 3[–8], syncarpous; styles 3[–5], free, very short, erect, recurved; stigma linear, papillate; ovary superior, 3-loculate; ovules numerous in each locule, the placentation axile. Fruit a thin-walled 3[–5]-loculate, ellipsoidal capsule, longer than and included within the persistent sepals, dehiscing loculicidally by 3[–5] persistent valves, the partitions separating from the persistent central axis bearing the funiculi of the ovules. Seeds numerous, somewhat compressed, reni-

[2] I could find no evidence in the many North American specimens of *Mollugo verticillata* in the Harvard University Herbaria (A, GH, NEBC) of the five white, petaloid staminodia described for this species by Ahles (in Radford, Ahles, & Bell, 1968).

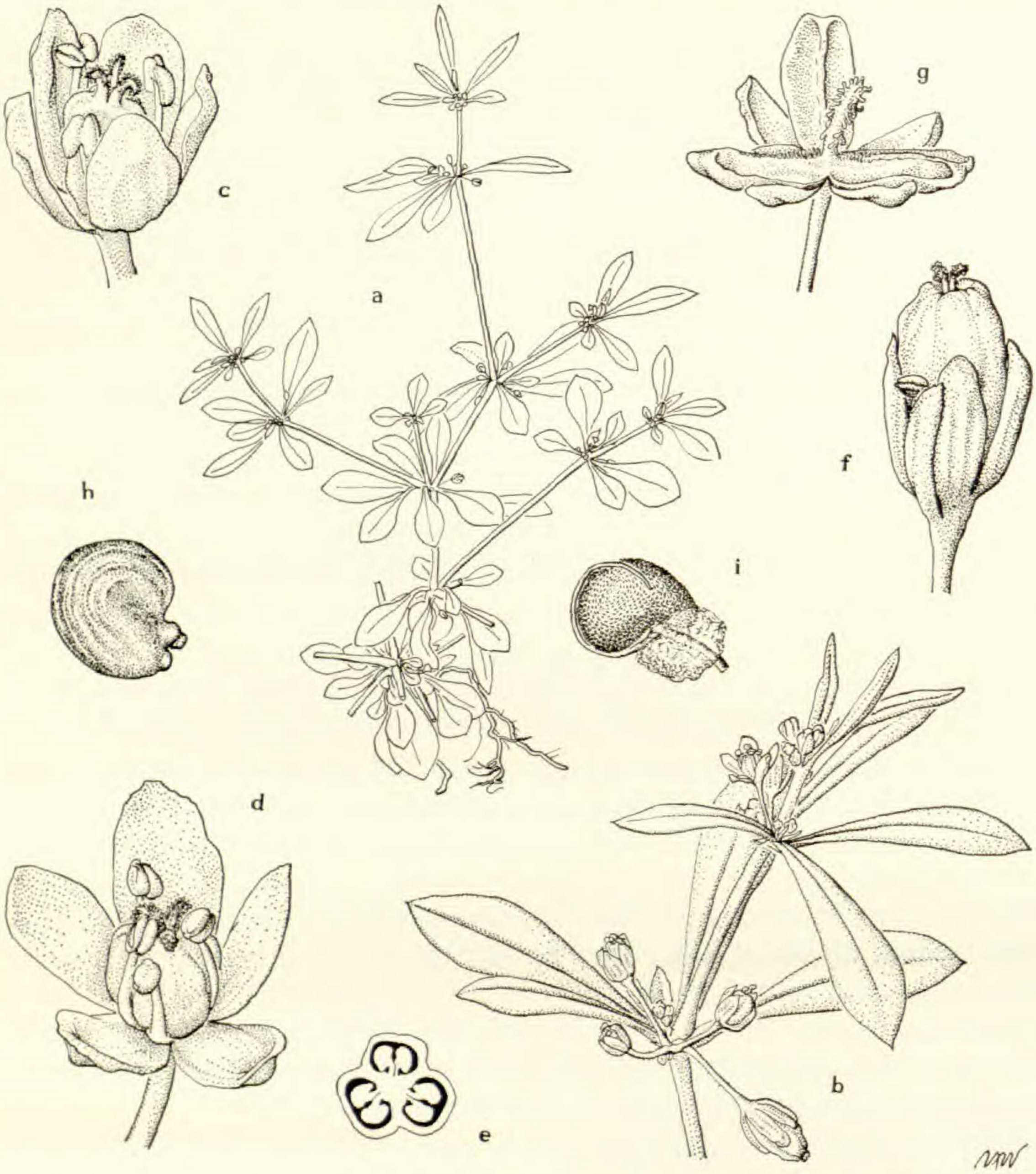


FIGURE 1. MOLLUGINACEAE. a–h, **Mollugo.** *M. verticillata*: a, part of a flowering plant, from above × ½; b, flowering and fruiting branch enlarged, × 4; c, flower, × 15; d, flower with forward sepals depressed to show enlarging superior ovary and hypogynous stamens, × 15; e, cross section of ovary showing placentation, × 15; f, mature fruit before dehiscence, with persistent sepals and stamens, × 8; g, fruit after dehiscence, × 8; h, seed with peglike hilum, × 25. i, **Glinus.** *G. lotoides*: seed — note long coiled appendage and inflated aril around funiculus, × 25.

form to roundish, reddish- to blackish-brown; seed-coat bearing 3–7 prominent to obscure longitudinal ridges or smooth; a distinct hilar peg present, but caruncle and filiform appendage lacking. Embryo peripheral, curved around a small amount of hard, semi-transparent endosperm; cotyledons oblong, fleshy. LECTOTYPE SPECIES: *M. verticillata* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 35. 1913. (An ancient generic name derived from Latin "*Mollitie plantae*", pliant or delicate

plants; see Linnaeus, Crit. Bot. 109. 1737; Philos. Bot. 157. 1751). — Carpet-weed, Indian chick-weed, Devil's grip.

A genus of about 35 species native to the tropics and subtropics of both hemispheres, but now widespread in temperate regions in North America and Europe as a weed of disturbed areas. Wilson lists nine species in the *North American Flora*, but these are mainly distributed in the West Indies and Central and South America. Only *Mollugo verticillata* L., $2n = 64$, occurs in our area, ranging from Florida northward through New England to Nova Scotia, westward to Ontario and North Dakota, southward to Texas, New Mexico, and Mexico, while on the Pacific coast it ranges from southern California northward to Oregon, Washington, and Idaho. A second species, *M. Cerviana* (L.) Seringe, $2n = 18$, ranging from Arizona to Lower California and Mexico, is distinguished from the relatively large, coarse, mat forming plants of *M. verticillata* by its small, ascending, diffuse habit, filiform stems, small linear leaves, long-pedicellate flowers usually with five stamens, and seeds with a reticulate seed-coat. This species has been reported to occur on ballast in the vicinity of New York City.

In our area *Mollugo verticillata* may occur in almost any disturbed situation, including cultivated ground, roadsides, railroad beds, sandy river banks, exposed lake-bottom muds, beaches, sand-dunes, and gardens. It flowers from spring to fall. Similar open or disturbed habitats are reported in autecological studies in India by Bakshi & Kapil on *M. Cerviana*, *M. nudicaulis* Lam., $2n = 54$, and "*M. hirta* Thunb." (= *Glinus lotoides* L.). The species are adapted to xerophytic conditions, with short life cycles that progress from germination after a few seasonal showers to flowering and fruiting within a few days, to death within 30 to 45 days. Self and insect pollination and wind dispersal of seeds are reported for these species.

The genera *Coelanthum*, *Glinus*, *Hypertelis*, and *Pharnaceum* are closely allied to *Mollugo*, which is possibly the most primitive of the group, being least specialized in habitat, habit, and floral structure (Adamson). The species of *Glinus* were treated by Bentham & Hooker and in parts of *Index Kewensis* as synonyms of *Mollugo*, an unfortunate taxonomic judgment that created much nomenclatural confusion in the literature.

Scattered chromosome counts for seven species of *Mollugo* indicate a polyploid series with diploid numbers of 18, 36, 54, and 64.

The genus has attracted relatively little interest. Howell described a complex of endemic evolution among eight closely related species in the Galapagos Islands in which two divergent lines have developed from a single variable glabrous annual prototype that had flowers with three or five stamens, a condition found in *M. verticillata*, to which the Galapagean species are "perhaps most closely related." Differentiation has resulted in "one line developing a subshrubby perennial habit and large flowers, the other line developing a low woody caudex and strikingly

glandular herbage. In both lines there is an increase in the number of stamens, approaching or equalling eight, the sum of the five stamens opposite the sepals and the three stamens alternate with the cells of the capsule, two staminal arrangements which occur in the *M. verticillata* type. The geographic separation of the several forms on the different islands has undoubtedly been an important factor in the segregation and maintenance of the specialized developments."

Payne described several interesting anatomical features exhibited by *Mollugo verticillata*, including an increase in thickness of the cortical tissues to produce swollen nodes, pseudoannulation in the xylem of the stems and roots, and the presence of rosettes of cells in the leaf epidermis representing vestigial trichome bases. Anomalous secondary thickening, reported by Metcalfe & Chalk (after Solereder) for "*M. radiata* R. & P." (= *Glinus radiata* (Ruiz & Pav.) Rohrb.) pertains to *Glinus* and has not been found in species of *Mollugo*. The floral vascular anatomy of three species of the genus has been described by Sharma. Excellent illustrations of the seeds of *M. verticillata* and *M. Cerviana* are provided by Thieret. Stomata of the ranunculaceous type occur on both surfaces of the leaves, while clustered and single crystals of calcium oxalate are found in tissues of the leaves and stems. Tartaric acid, tannins, and bitter glucosides, but no alkaloids, have been found in *M. nudicaulis*. Pollen grains with four germ pores and a two-celled condition at shedding are recorded for *M. verticillata* (Payne), in contrast to the three-celled condition reported elsewhere in the family, and Sharma reports pollen grains three-colporoidate in *M. nudicaulis*, and three- to five-zonicolporoidate in *M. pentaphylla* L.

Embryological studies by Payne (*Mollugo verticillata*), Bhargava (*M. nudicaulis*), and Kshirsagar (*M. stricta* L.), indicate that ovules are anacampylotropous at fertilization. Embryo-sac development is normal (Polygonum type), while development of the embryo is probably of the solanad type. Endosperm formation is initially free-nuclear, later becoming cellular.

The genus is of no economic importance. Plants of *Mollugo Cerviana* and *M. pentaphylla* are used in the Old World as a vegetable and in folk medicine against a wide variety of complaints, including skin disorders and diarrhoea, or as a mild laxative.

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3. **Glinus** Linnaeus, Sp. Pl. 1: 463. 1753; Gen. Pl. ed. 5. 208. 1754.

Annual herbs, with radiating, much-branched, procumbent to ascending stems, forming mats up to 0.5 m. in diameter. Foliage and axes covered with a dense, short, whitish, stellate pubescence, particularly when young [or glabrous]. Leaves alternate to whorled, exstipulate, unequal, entire, ± fleshy, elliptic to ovate, spatulate, obovate or orbicular, gradually narrowed below to a slender petiole, apex rounded to abruptly acute. Inflorescence a dense, sessile to short-pedunculate axillary dichasium. Flowers few to numerous, sessile to short pedicellate. Sepals 5, free, externally stellate-tomentose, margins hyaline, tip mucronate, aestivation quincuncial, persistent. Stamens (3–)5[–20], alternate with and shorter than the sepals [or fascicled when numerous], hypogynous; filament filiform, anther versatile, 2-loculate at anthesis, the 2 lobes separated above and below the point of insertion, dehiscence dorsilateral by longitudinal slits. Carpels 3(–5), united; styles wanting; stigmas 3(–5), sessile, of hyaline papillae, persistent [or styles 3–5, short, erect]; ovules numer-

ous, anacampylotropous, the placentation axile. Fruit an ovoid, loculicidal capsule, the 3(–5) valves separating from a central axis bearing the funiculi and sterile ovules. Seeds numerous, reniform, with a short funiculus enclosed within a bladder-like caruncle and a long filiform appendage coiled round the seed; seed-coat tuberculate to nearly or quite smooth and shiny, reddish- to blackish-brown. Embryo curved; cotyledons oblong, fleshy, endosperm starchy. TYPE SPECIES: *G. lotoides* L. (Name from Greek *glinos*, sweet juice, the significance not clear.)

A genus of about thirteen species with pantropical distribution, reaching temperate areas as an introduced weed. Two species are found in our area. *Glinus lotoides* L., with obovate to orbicular leaves and usually tuberculate seeds, has been found from Louisiana (Thieret) to Oklahoma, Arkansas, and Missouri, in moist situations on alluvial muds and sands on the margins of rivers and lakes, as well as on moist forest soils. *Glinus radiatus* (Ruiz & Pav.) Rohrb., with narrower leaves and smooth seeds, is reported from Louisiana, Oklahoma, and California, southward in Mexico to Central America, and in the West Indies. These two species are distinguished primarily on the texture of the seed coat (cf. Wilson), but the limits of their variation and distribution in the southern United States appear rather indefinite, suggesting the need for further collection and study.

Although considered distinct by Linnaeus, *Glinus* was later reduced to synonymy under *Mollugo* L. by Bentham & Hooker and in the earlier volumes of the *Index Kewensis*. The extensive and very confusing synonymy which resulted is discussed in detail by Pitot. *Glinus lotoides* frequently appears under the synonym *Mollugo hirta* Thunb. The genera are now generally accepted as distinct, with *Glinus* differing from *Mollugo* principally in the presence of a conspicuous caruncle and a filiform appendage (frequently mistaken for the funiculus) on the seed, and in the dense stellate pubescence of *Glinus*. Adamson (1960) suggests that *Glinus* was derived from the same stock as *Mollugo*, but along a distinct line, and that the Brazilian *Glischrothamnus* Pilg. is derived from *Glinus*.

Chromosome counts of $2n = 36$ have been reported for both *Glinus lotoides* and *G. oppositifolius* (L.) A. DC. The report by Solereder (repeated in Metcalfe & Chalk) of anomalous secondary thickening in stems and roots of *G. radiatus* (as *Mollugo radiata* Ruiz & Pav.) should perhaps be reconfirmed. Both anomocytic and paracytic stomatal types occur in the leaf epidermis (Inamdar). The floral vascular anatomy of *G. lotoides* and *G. oppositifolius* is described by Sharma. The embryology of only *G. lotoides* is known. The walls of the tetrasporangiate anther are four cell-layers thick. The cells of the single tapetal layer each contain two to three many-nucleolated nuclei. Mature pollen grains are tricolpate (Sharma), and distinctly three-celled when shed. Ovules are anacampylotropous and crassinucellate, with two integuments. The caruncle (or "aril") may finally enclose as much as the lower third of the ovule in some instances, but its size varies in different specimens, and seeds of

*G. lotoides* lacking the caruncle are illustrated by Pitot. Embryo-sac development is of the Polygonum type, and the mature embryo sac contains abundant starch grains.

The genus is of no commercial value. In India the leaves of *Glinus lotoides* and *G. oppositifolia* are used as a vegetable or as an appetizer. As an herb the plants are used as a purgative or as a remedy for diarrhoea, itches, and skin diseases.

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## AIZOACEAE Rudolphi, Syst. Orb. Veg. 53. 1830, "Aizoideae" [C. Sprengel, Anleit. ed. 2. **2**(2): 842. 1818, "Aizoiden"], nom. cons.

(MESEMBRYANTHEMUM FAMILY)

Slightly fleshy to markedly succulent annual or perennial herbs and low subshrubs [or shrubs], with glabrous, papillose, or pubescent, prostrate to erect and usually much-branched stems spreading from a small, narrow taproot, often forming mats. Leaves ± succulent, cauline, alternate or opposite, stipulate or exstipulate, sessile or petiolate, the petioles often dilated, the membranaceous margins sometimes decurrent, or connate in a sheath about the node; blades simple, entire, flattened to ± cylindrical, glabrous, papillate or pubescent. Flowers mostly inconspicuous, regular, perfect; axillary or terminal (but appearing axillary), sessile to pedicel-

late, solitary, paired, or few in a cymose or spike-like cluster [or inflorescence a dichasium], often flanked by a pair of small, sessile, marcescent bracts. Sepals (tepals) (3–)5, equal or unequal, united below in a usually shallow tube, the tube free from or united with the ovary, the lobes imbricate or quincuncial, erect, hooded or incurved above, ± fleshy, sometimes keeled and bearing a subapical dorsal appendage, greenish without, white or pink to purplish within, persistent or falling as a unit. Petals none [or few to numerous, staminodial, often colorful]. Stamens (1–)3, 5, (7–)10(–13), to numerous, solitary or in pairs or groups alternate with and opposite the calyx lobes or in a continuous cycle, free or united basally, inserted on the floral tube, persistent or falling with the sepals; anthers 4-sporangiate, 2-loculate at anthesis; pollen mostly 3-colpate or colporoidate. Carpels rarely 1 or 2, usually 3–5[–20], united; styles as many as the carpels, free or united below; ovary superior or half-inferior [to inferior], 1–5-loculate or incompletely 2-chambered by a horizontal partition; placentation axile, basal, or parietal, ovules 1 to numerous, campylotropous, arillate or exarillate. Fruit a loculicidal or circumscissile capsule or bony and indehiscent, bearing several sharp horns. Seeds 1 to numerous, small, ± reniform to pyriform, smooth to wrinkled or tuberculate-striate, brown to black; embryo ± curved to annular; endosperm starchy, hard and semitransparent or soft and white. TYPE GENUS: *Aizoön* L.

A family of about eleven more or less weedy genera (including *Tetragonia* and *Mesembryanthemum, sensu lato*, but excluding the fourteen genera now segregated in the Molluginaceae) and approximately 2500 species, with a primary center of distribution in South Africa, but also well developed in the Mediterranean region and Australia, and distributed in dry regions of the tropics and subtropics of both hemispheres. Five genera (*Cypselea, Galenia, Sesuvium, Tetragonia, Trianthema*), and six species occur in our area, mainly as strand plants or weeds of waste places.[3]

Only two of the six subfamilies now recognized in the family (Schwantes, Eckardt) reach our area: the monotypic Tetragonioideae Lindl., with apetalous flowers, half-inferior ovaries, and stony indehiscent fruits, and the Aizoöideae, containing ten apetalous genera with superior ovaries and capsular fruits. The subfamilies Aptenioideae, Hymenogynoideae, Caryotophoroideae, and Ruschioideae are either largely or entirely confined to Africa. The family appears to reach an evolutionary climax in the genus *Mesembryanthemum, sensu lato*, with its many curious, strongly succulent plants and striking flowers with many colorful petaloid staminodia. *Mesembryanthemum* has been split into about 120 segregate genera

[3] The monotypic genus *Geocarpon* Mackenzie, disjunctly distributed in southwestern Missouri (Greene, Jasper, Polk, and St. Clair counties) and southeastern Arkansas (Drew and Bradley counties), and cited under Aizoaceae by various authors (Fernald, Gleason, Pax & Hoffmann, Wilson), has been transferred to Caryophyllaceae by Palmer & Steyermark (1950) as the type of a monotypic tribe Geocarpeae (in subfam. Alsinoideae).

and elevated to family rank (see Ihlenfeldt, Schwantes & Straka, 1962; Eckardt, 1964; Pax & Hoffmann, 1934; for literature citations and accounts of the systematics of this diffcult group).

In the older, more conservative sense the Aizoaceae consisted of a broad and ill-defined alliance of about 25 genera (including those now placed in Molluginaceae) that has appeared in the literature under several family names, including Aizoaceae (Pax, Pax & Hoffmann), Ficoidaceae (Bentham & Hooker, De Candolle, Jussieu), Sesuviaceae (Horaninow), and Tetragoniaceae (Small, Wilson). The question of the correct family name has been problematical (cf. Sprague, Rowley, Friedrich), but Aizoaceae is now conserved. In the older literature various genera have been attributed to such related families as Caryophyllaceae, Phytolaccaceae, and Portulacaceae, or more recently placed in segregate families such as Molluginaceae Hutchinson, *nom. cons.* (Rohrbach), Mesembryanthemaceae Fenzl, *nom. cons.* (Lindley; Endlicher; Ihlenfeldt, Schwantes, & Straka; Schwantes), or Tetragoniaceae Nakai, *sensu stricto, nom. cons.* Two families, Molluginaceae and Aizoaceae (or Ficoidaceae, including *Mesembryanthemum* and *Tetragonia*), are most often recognized in the recent literature (Cronquist, Eckardt, Adamson, Hutchinson, Friedrich).

The Aizoaceae are distinguished from the Molluginaceae by their characteristically succulent habit, sepals united basally to form a calyx tube, stamens inserted perigynously, and ovary often partly or entirely inferior; by the presence of betacyanin pigments (betalains, reported thus far for 13 genera and 36 species) rather than anthocyanins; and by the frequent occurrence of anomalous secondary growth in stems and roots. The family has long been considered to have been derived from a phytolaccaceous stock, and it is closely related to the Portulacaceae through *Sesuvium* and *Trianthema*. Relationships to the Cactaceae have also been proposed (Buxbaum).

Available chromosome counts indicate a base number of $x = 8$ (or 9) for the "semi-succulent" group (including *Sesuvium*, *Tetragonia*, and *Trianthema*), with diploid numbers of $2n = 16$, 26, 28, 32, 36, 48, and 96; while $x = 9$ for the "succulent" group (largely confined to Africa), with numerous counts of $2n = 18$, 27, 36, 54, 72, and 108 (Darlington & Wylie).

The embryology of the family has not been intensively studied. Available details include tetrasporangiate anthers, with development of the Basic type and containing Ubisch granules (*Sesuvium Portulacastrum*), and pollen grains three colpate (Sharma) and three-celled when shed. Ovules are anacampylotropous to campylotropous and crassinucellar, with the micropyle formed by the inner of two integuments. A third integument or aril, is reported in *Galenia*, *Sesuvium*, and *Trianthema*. Embryosac development is of the Polygonum type (but the Adoxa type has been described for *Mesembryanthemum pseudotruncatellum*). Starch grains are present in the mature embryo sac. Endosperm formation is initially nuclear, becoming cellular (but remaining nuclear up to eleven days after pollination in *Trianthema Portulacastrum*). Embryo development is of

the solanad type, and polyembryony has been reported in *Trianthema Portulacastrum* (Davis).

In a study of the floral vascular anatomy of species of *Galenia*, *Sesuvium*, and *Trianthema*, Sharma (1962) found progressive fusion of the "tepals," and increasing adnation between the perianth tube and the stamen filaments. These trends are accompanied by progressive stelar condensation in the receptacle, resulting in a transition from independent origins of the tepal and stamen traces, to their adnation and origin as common bundles. He concluded that specialization in the androecium among these species has resulted in a reduction from numerous to few stamens, rather than in an increase in number via "dédoublement." In all species the carpel walls were supplied with five or more bundles (as opposed to three in the Molluginaceae), a condition which he considered derived. He considered the "Ficoidaceae" advanced over the Molluginaceae in the possession of fused tepals whose traces arise at the same level from the stele and divide within the receptacular cortex; perigynous stamens; semi-inferior to inferior ovaries whose carpellary traces divide before leaving the cortex; and fewer ovules. The organogeny of the flower in *Tetragonia* and *Trianthema* has been described in detail by Payer.

The family is of economic significance primarily for the many species of *Mesembryanthemum* and related genera cultivated as ornamentals, and for the various species of *Sesuvium*, *Tetragonia*, and *Trianthema* cultivated for use as vegetables or in folk medicine.

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## KEY TO THE GENERA OF AIZOACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *fleshy to strongly succulent, glabrous or pubescent, prostrate or erect herbs; stems often much branched and forming mats; leaves cauline, alternate or opposite, simple, entire, flattened or nearly cylindrical, often with dilated petioles, stipulate or exstipulate; flowers small and inconspicuous, axillary, solitary or clustered, ± sessile, regular, perfect; sepals 3–5, united below into a shallow floral tube, the lobes green, white, pink or purplish within; petals none; stamens mostly 3–10 or numerous, solitary, paired, or in groups, alternate with or opposite the sepals; ovary superior or semi-inferior, 1–5 locular; carpels 1–5, united; ovules and seeds 1–many; placentation axile, basal, or parietal; fruit a loculicidal or circumscissile capsule or bony and indehiscent; seeds reniform to pyriform; seedcoat smooth, wrinkled or tuberculate.*

A. Ovary superior; fruit a loculicidal or circumscissile capsule; leaves alternate or opposite.
  B. Capsule loculicidal by 3–5 valves; ovules and seeds solitary; stamens 8–10, in pairs alternate with the sepals; stems and alternate leaves densely white-pubescent; stipules absent. ..... 1. *Galenia.*
  B. Capsule circumscissile; ovules and seeds few to numerous; stamens 1 to many; leaves opposite.
    C. Ovary 3–5-loculate; seeds numerous; stamens 5 to many; sepals appendaged, persistent; leaves ± equal; stipules absent. ..... 2. *Sesuvium.*
    C. Ovary 1- or 2-loculate; leaves unequal; stipules present.
      D. Stamens 5–10; sepals appendaged; ovules and seeds few; cap of the ovary fleshy and crested; stipules scarious. ..... 3. *Trianthema.*
      D. Stamens 1–3(–5); sepals unappendaged; seeds numerous; cap of the ovary thin-walled and rounded; stipules laciniate. ..... 4. *Cypselea.*

A. Ovary half-inferior; fruit horned, indehiscent, bony; leaves alternate, exstipulate, the blades flat, ± ovate-triangular, papillose. . . . . 5. *Tetragonia.*

Subfamily AIZOÖIDEAE [Schwantes]

1. **Galenia** Linnaeus, Sp. Pl. 1: 359. 1753; Gen. Pl. ed. 5. 169. 1754.

Perennial, much-branched, grayish [or yellowish to green], prostrate [or erect] herbs or subshrubs [or shrubs]; branches woody at the base, forming dense mats, lateral branches alternate, ± secund, spreading; stems and leaves initially densely coarsely villous with loosely appressed, whitish, flattened hairs, becoming ± glabrescent. Leaves alternate [or opposite], secund, entire, fleshy, sessile exstipulate, the epidermis coarsely papillose; leaves variable in size, those of the main stems largest, with blades broadly obovate, tapering below to a broad base, the apex obtuse, younger leaves ± elliptic to obovate and acute. Flowers small and inconspicuous, on short lateral branches, sessile, axillary, solitary or in groups of 2–5 [or inflorescence a terminal, paniculate cyme]. Sepals (4) 5, united below in a shallow floral tube, the lobes erect, the tips curved inward and downward, pubescent without, glabrous and whitish within. Stamens (8–)10, of unequal length, inserted on the floral tube in pairs alternate with and shorter than the calyx lobes; anthers small, yellow; filaments flat, tapering upwards [or filiform]; pollen 3-colpate. Gynoecium of [2–]3–5 united carpels; styles [2–]3–5, free or united below, stigmatic along the inner surface; ovary superior, truncate and [2–]3–5-angled above, the center depressed, 3–5-loculate [or 2- or 1-loculate by abortion]; placentation axile; ovule solitary in each cell, pendulous on an arching funiculus, campylotropous. Fruit a small, leathery, [2–]3–5-angled capsule with depressed apex, dehiscing loculicidally from the top [or indehiscent]. TYPE SPECIES: *G. africana* L. (Named for Claudius Galenus, ca. 130–ca. 200 A.D., noted Greek naturalist and physician of Pergamos in Asia Minor.)

A genus of about 27 species with a natural distribution confined to southern Africa. The genus is represented in our area by one adventive species, *Galenia secunda* (L. f.) Sond. (subg. KOLLERIA), which can be recognized by its prostrate and secund habit, small axillary flowers, paired stamens, superior 5-angled ovary, and one-seeded carpels. The species is represented in the Harvard University Herbaria by only two sheets of a collection by A. H. Curtis (no. *6869*, in 1901) from Pensacola, Florida. In a penned note accompanying one of these Curtis states that "of my Pensacola plants none but #6865 grew on strictly ballast ground, but the seeds of most of them doubtless came in ballast — No. 6869 forms dense mats probably 4 ft. across. Leaves thickish & with cinereous color." These specimens bear flowers but no fruits. Small described the ovary of this species as partly inferior, but in the specimens at hand, and as described by Adamson, the ovary is superior. Seeds from a South African specimen of the species are small, compressed, and semilunate in outline, with a

coriaceous, iridescent blackish-brown seed coat with longitudinal, tuberculate striations. The embryo is curved around a copious starchy endosperm (but is not nearly annular), and has oblong, fleshy cotyledons about as long as the radicle. The continued presence of the genus in our area needs confirmation. A chromosome count for the genus is lacking.

Two subgenera (Fenzl, Sonder, Adamson) or sections (Pax, Pax & Hoffmann) have been consistently recognized in the genus. The composition of the subgenera (GALENIA and KOLLERIA Fenzl) has been emended by Adamson in the only recent treatment of the genus. *Galenia* is closely related to the South African genus *Plinthus* Fenzl, the two forming a group within the tribe Aizoëae (Adamson).

The pubescence in our specimens is simple, but two-armed hairs occur in some species of the genus. Large bladder-like water storage cells are present in the leaf epidermis. In the dried specimens these collapse, giving the leaf surface a pitted appearance. Delicate spiral thickenings of the vessel walls and anomalous secondary thickening are reported for the genus (Metcalfe & Chalk).

The genus is of no economic significance. *Galenia spathulata* Fenzl may be used as fodder for sheep in southern Africa.

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2. **Sesuvium** Linnaeus, Syst. Nat. ed. 10. 1052, 1058, 1371. 1759.

Annual or perennial, prostrate or ascending, succulent, glabrous herbs or subshrubs. Stems several from a short tap-root, sometimes rooting at the nodes, often reddish, branching alternately. Roots fibrous. Leaves opposite, ± equal, entire; blades nearly cylindrical to ± flattened, linear-lanceolate to elliptic or obovate; apex acute or obtuse; petioles dilated, the membranaceous margins clasping [or connate], exstipulate. Flowers perfect, terminal but appearing axillary, solitary or clustered, sessile to long pedicellate, a pair of marcescent bracteoles at the base of the pedicel. Sepals 5, united below, the lobes imbricate, margins scarious, hooded above and bearing a short subapical dorsal mucro, pink to lavender within, spreading at anthesis, persistent. Stamens 5, free and alternisepalous or numerous in groups alternate with the sepals or in a continuous cycle, inserted on the floral tube, shorter than the sepals, persistent; filaments filiform or subulate; anthers small, often reddish; pollen tricolpate [or polymorphous?]. Styles 2–5, linear, erect; stigma longitudinal, papillose;

ovary superior, 2–5 loculate; ovules numerous, anacampylotropous, placentation axile. Capsule membranaceous, enclosed within the persistent perianth, circumscissile near the middle. Seeds numerous, small, roundreniform, smooth, lustrous, black, arillate, the aril membranaceous, tightly investing the seed; embryo annular or slightly coiled; cotyledons oblong, fleshy; endosperm soft, starchy. (Including *Halimum* Loefl., *Halimus* Kuntze, *Squibbia* Raf.) TYPE SPECIES: *S. Portulacastrum* (L.) L. (Name Latin, presumably after *Sesuvium*, land of the Sesuvii, a Gallic tribe, the significance here not explained.) — SEA PURSLANE.

A genus of about eight species distributed in the tropics and subtropics of both hemispheres, inhabiting saline beach-dunes, marshes, hammocks, and disturbed situations in coastal areas. Two rather variable species occur in our area. *Sesuvium maritimum* (Walt.) BSP. (*S. pentandrum* Ell.) with flowers small and sessile or nearly so and five alternisepalous stamens, ranges from Long Island southward to Florida and the West Indies, westward to northern Louisiana and Texas. *Sesuvium Portulacastrum* (*S. sessile* Pers.) $2n = 16, 36, 48$, with larger and distinctly pedicellate flowers and numerous stamens, appears to occur sporadically in the Carolinas, and from Georgia southward through Florida to the West Indies, westward to Texas, and southward to Mexico, Central America, and South America. *Sesuvium crithmoides* Welw., a native of Angola, with long, narrowly linear leaves and sessile flowers, was collected once in 1902 on the waterfront in Brunswick, Georgia, but has not been reported since. In the southwestern United States *Sesuvium verrucosum* Raf., with an often more erect habit, numerous stamens, and vegetative surfaces densely papillate with large epidermal water-storage cells, approaching our area in Oklahoma and Texas, ranges northward and westward through Kansas, Colorado, Utah, Nevada, and central California, and southward to Mexico.

*Sesuvium* is closely related to *Cypselea* Turp. and *Trianthema* L. It has been recognized as distinct by all authors except Degener & Degener, who reduce it to synonymy under *Trianthema*, stating that the difference between the two genera is mainly "the number of cells in the ovary, a character . . . of trivial importance." These three genera have been consistently allied, and the group is thought to link the Aizoaceae to the Portulacaceae.

Chromosome counts, available only for *Sesuvium Portulacastrum*, indicate the presence of polyploidy and aneuploidy, with base numbers of eight (and nine), and $2n = 16, 32, 36, 48$. The presence of betacyanin has been demonstrated in *S. Portulacastrum*.

Species of *Sesuvium* exhibit structural adaptations to xerophytic conditions. The succulent leaves of *S. Portulacastrum* have stomata on both surfaces and contain subepidermal palisade tissues that are four to five cell-layers thick and enclose a central zone of loose, water-storing parenchyma. In contrast, the leaves of *S. maritimum* contain a homogeneous chlorenchyma interrupted only by large intercellular spaces that underlie

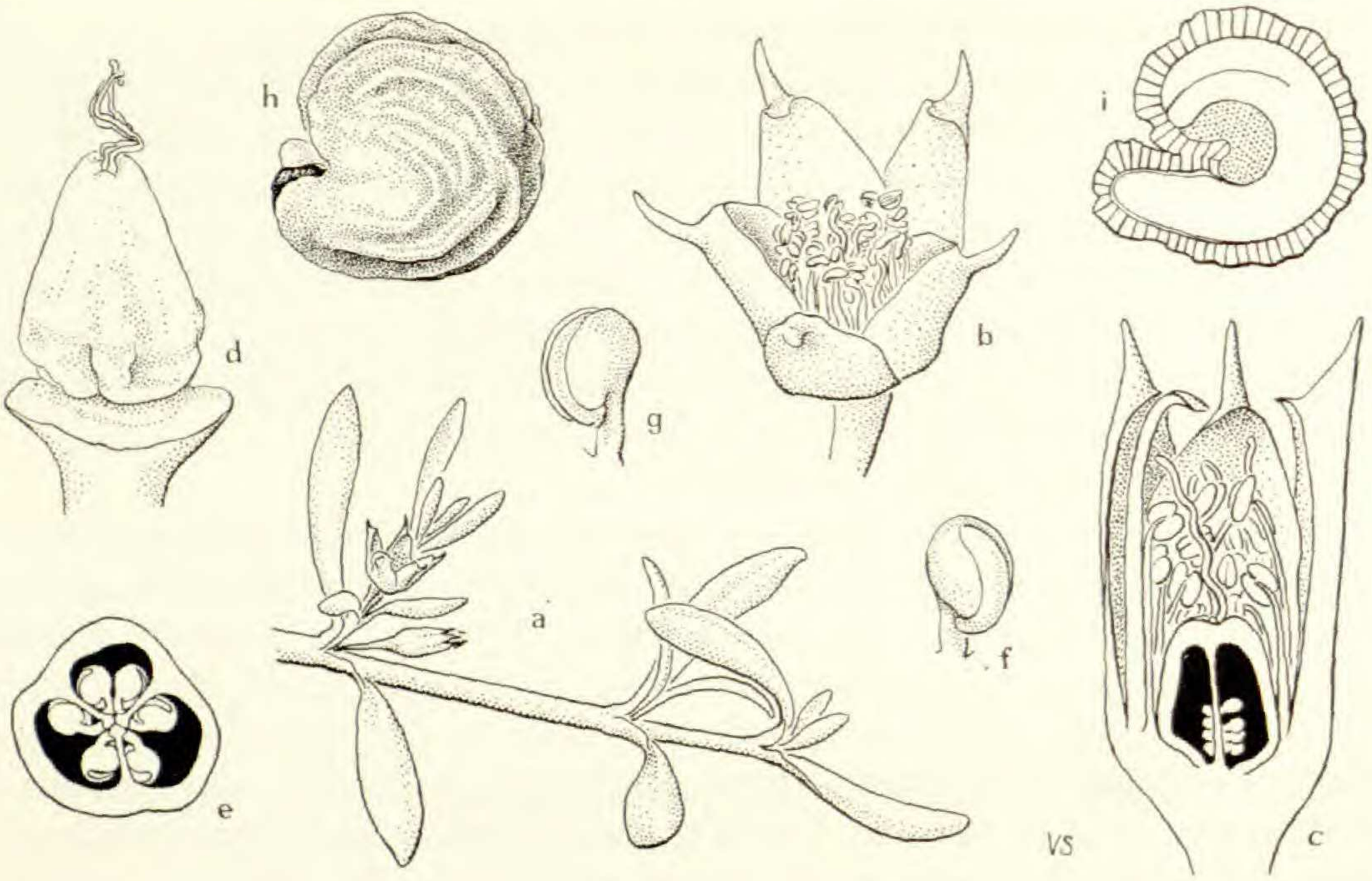


FIGURE 2. **Sesuvium.** a–i, *S. Portulacastrum*: a, flowering branch, × ¾; b, flower, × 3; c, flower in semidiagrammatic vertical section to show slightly perigynous insertion of floral parts, superior ovary, and placentation, × 5; d, mature fruit before dehiscence, perianth removed, × 4; e, cross section of ovary showing three septa and parietal placentation, × 10; f, g, lateral views of ovules at or near anthesis showing aril developing from funiculus, × 25; h, mature seed — note tightly investing membranaceous aril, × 20; i, seed in section, showing curved embryo surrounding endosperm (stippled), diagrammatic, × 20.

large water-storage cells in the epidermis. The epidermal cells have a thickened outer wall with a smooth cuticle. Stomata are of the ranunculaceous type. Crystal clusters occur in cells of the pith, cortex, and leaves. Anomalous secondary thickening is reported in the stems and roots of *S. Portulacastrum*.

The ovules of *Sesuvium Portulacastrum* have two integuments (the inner of which forms the micropyle) and an aril (or third integument). The inner integument is two cell-layers thick, the second integument is initially two layers thick but becomes three layered, while the aril is three cell-layers thick. A Polygonum-type embryo sac is formed, and embryo development probably conforms to the Linum variation of the solanad type. The nucellus immediately above the embryo sac consists of two to three layers of radially elongate cells, while five to six cell-layers are present along the sides of the sac. The endosperm is initially free nuclear, but later becomes cellular. Anthers are tetrasporangiate, with walls five cell-layers thick, the innermost layer forming a glandular, binucleate tapetum. Ubisch bodies are present in the anthers. Pollen grains are three celled when shed.

*Sesuvium Portulacastrum* is cultivated as a vegetable in some Asian countries.

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3. **Trianthema** Linnaeus, Sp. Pl. **1**: 223. 1753; Gen. Pl. ed. 5. 105. 1754.

Succulent, glabrous [or pubescent], herbaceous or suffrutescent, annual or perennial plants of waste places. Stems prostrate or erect, from a short tapering taproot, often much branched, the branches alternate or opposite and usually bearing decurrent lines of hairs from the petiolar sheath to the node below, glabrescent. Leaves opposite, the members of a pair conspicuously unequal; blades glabrous, fleshy, elliptic-lanceolate to spatulate, obovate, or suborbicular, the apex acute or obtuse to truncate-acuminate or retuse, the base acutely tapering to rounded; petiole margins expanded, membranaceous, connate into a sheath around the node, stipulate. Flowers axillary, solitary or cymosely clustered [or inflorescence a dichasium], sessile or short-pedicellate, perfect. Sepals 5, united below and falling as a unit [or persistent], the tube fused with two bracteoles, the petiolar sheath, and even the stem, the lobes imbricate, cucullate, with a sometimes-barbed dorsal mucro just below the apex [or mucro absent], inner surface colored bright- to purplish-pink [or white]. Stamens 5–10, inserted on the floral tube in two cycles alternate and opposite the sepals [or stamens 1–3 or numerous in fascicles alternate with the sepals], shorter than and falling with the sepals; anthers small, rotund

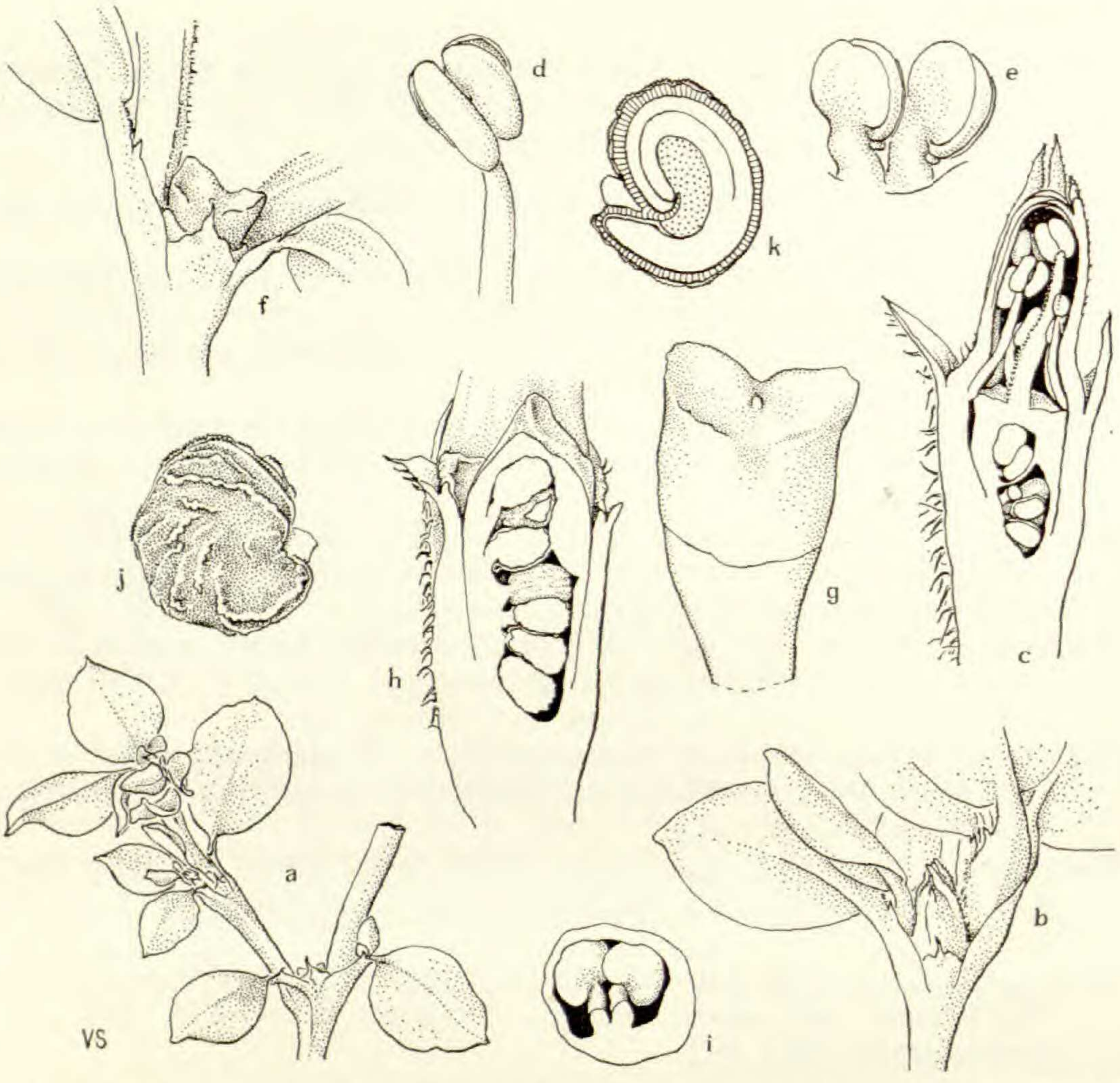


FIGURE 3. **Trianthema.** a–k, *T. Portulacastrum*: a, flowering branch, the axillary flowers hidden by the fused sheathing leaf bases and secondary bracts, × 1; b, an axillary flower with connivent calyx lobes — note sharply pointed secondary bract in foreground between petioles, × 3; c, flower in semidiagrammatic vertical section to show connate sepals, perigynous insertion of floral parts, semi-inferior ovary, parietal placentation, and horizontal septation of locule, × 7; d, stamen, × 20; e, lateral view of two ovules — note aril developing from funiculus, × 30; f, nearly mature fruit inclosed by tube consisting of fused leaf bases, secondary bracts, and perianth — note fleshy cap protruding, × 3; g, same, floral tube removed — note horizontal line of dehiscence between fleshy cap and membranaceous base of pyxis, × 7; h, fruit in semidiagrammatic vertical section, × 5; i, cross section of ovary, showing parietal placentation, × 6; j, seed with tightly investing aril, × 12; k, seed in section, showing curved embryo inclosing endosperm (stippled), × 12.

to oblong; filament filiform; pollen tricolpate. Style 1[–2], short (in ours), excentric; stigma longitudinal, papillate; ovary superior, one or incompletely 2-chambered by a horizontal partition, ± truncate above and bearing an excentric, often bilobed marginal crest [or peripheral corona]; ovules few, campylotropous, arillate, placentation basal or parietal. Capsule superior, ± turbinate, closely surrounded below by the floral tube, walls membranaceous below but fleshy above, apex truncate,

circumscissile near the middle, the fleshy cap exserted and bearing a bilobed marginal crest and including the upper chamber of the ovary. Seeds [1–]several, round-reniform, arillate, wrinkled, reddish-brown to black, the upper 1 or 2 often enclosed in the upper chamber of the ovary and falling with the indehiscent operculum, 2 or more remaining in the lower chamber. Embryo annular to slightly coiled, surrounding the starchy endosperm; cotyledons oblong, fleshy. (Including *Portulacastrum* Juss.). TYPE SPECIES: *T. Portulacastrum* L., $2n = 26$. (Name derived from Greek *treis*, three, and *anthemon*, flower.) — SEA PURSLANE, HORSE PURSLANE.

A small pantropical genus of perhaps 25 species inhabiting sandy seabeaches, hammocks, alkaline or clay soils, and waste places where introduced. The genus has centers of development in Africa and Australia and is represented in our area only by *Trianthema Portulacastrum*, which ranges from New Jersey to Florida and the West Indies, westward to Texas and southern California, northward to Oklahoma and Missouri, and southward to Mexico and Central and South America. The species is quite variable in habit, pubescence, development of the inflorescence, length of the bracteoles and sepals, number and length of stamens, and form of the crest of the operculum.

Two sections were recognized in the genus in De Candolle's *Prodromus* (sect. ZALEYA Burm. f. and sect. ROCAMA Forsk., which included *Trianthema Portulacastrum*). More recently Jeffrey (followed by Adamson) has recognized two subgenera: TRIANTHEMA, with flowers usually solitary and ovaries containing four to numerous ovules, and PAPULARIA (Forsk.) Jeffrey with flowers usually clustered and ovaries containing two superposed ovules. Jeffrey resolved the confused generic limits between *Trianthema* and *Sesuvium* in Africa by reestablishing the genus *Zaleya* Burm. f. to contain the digynous species *T. decandra* L. (locules and stigmas two, operculum two valved). *Trianthema* is also closely related to *Cypselea* Turp.

The few chromosome counts available suggest the development of polyploidy and aneuploidy within the genus, since $2n = 16$ in *Trianthema argentina* Hunziker & Cocucci, *T. decandra*, *T. pentandra* L., and *T. polysperma* Hochst., while $2n = 26$ and 36 in *T. Portulacastrum* (as *T. monogyna*), and $2n = 28$ and 32 in *T. crystallina* Vahl. A relationship between level of ploidy and ecological characteristics in several African species is suggested by Hagerup.

Morphological adaptations to xerophytic conditions are apparent in the leaf structure of *Trianthema Portulacastrum*, in which a central, compact, palisade-like chlorenchyma tissue is bounded above and below by one or two layers of thin-walled water-storage cells and the epidermal layers are uncutinized. Stomata (both anomocytic and paracytic types: Inamdar) occur on both surfaces of the leaf. The upper epidermis consists of large, angular, thin-walled cells, and bladder-like epidermal cells are recorded in *T. crystallina* Vahl. The leaf veins are surrounded by a sheath of

parenchyma cells that lack chloroplasts but contain abundant starch grains. Drusiform clusters of calcium oxalate crystals are abundant in the parenchymatous tissues of the leaf and stem of *T. Portulacastrum*. Anomalous secondary thickening has been reported in *Trianthema*, but its occurrence should perhaps be confirmed.

Embryological studies of *Trianthema argentina*, *T. decandra*, and *T. Portulacastrum* (as *T. monogyna* L.) indicate that ovules are either campylotropous or amphitropous and have a bulky nucellus surrounded by two integuments (the inner of which forms the micropyle) and an aril or "third integument." In *T. argentina* a characteristic air space is reported between the inner and outer integuments at the chalazal end of the ovule, and the cells of the nucellar epidermis are reported to elongate and undergo periclinal divisions to form the nucellar cap (Cocucci), while in *T. Portulacastrum* the epidermal cells are said merely to stretch out radially (Bhargava). Embryo-sac development is of the Polygonum type, and starch grains accumulate in the embryo sac. The endosperm is initially nuclear, but later becomes cellular from the micropylar end. Development of the embryo is of the solanad type (probably the Linum variation). Polyembryony has been reported in *T. Portulacastrum*. The anther walls develop normally and contain five cell-layers at maturity, including a binucleate cellular tapetum. Pollen grains are three celled when shed.

The alkaloid trianthemin (of unknown structure) has been isolated from the Indian drug "punarnava," which is derived from *Trianthema Portulacastrum* (*T. monogyna*) and is used in the Ayurvedic medicine of India in cases of heart disease, anemia, and other disorders. The presence of betacyanin has also been demonstrated in this species.

The genus is of no commercial value, but some species are cultivated as vegetables in eastern Asia. Leaves of *Trianthema Portulacastrum* are used as a vegetable in India and Africa, and a decoction of its roots serves as an emenagogue in the Philippines and may be abortive in large doses. Its root is also used as an amenorrheic or as a cathartic in powdered form with ginger. Ashes of the herbaceous *T. salsoloides* Fenzl are mixed with simson oil and lime in Sudan to make a soap. Plants of *T. pentandra* L. are also used in Sudan as an astringent in abdominal diseases, while the leaves are eaten as a potherb in times of famine, and ashes of the plant are a source of salt for the natives (Uphof). Several species of the genus, including *T. Portulacastrum*, are reputed to be poisonous to livestock because of their content of alkaloids, oxalates, saponins, or nitrates.

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4. **Cypselea** Turpin, Ann. Mus. Hist. Nat. Paris 7: 219, *pl. 12*, *figs. 0–11*. 1806.

Small, prostrate, glabrous to papillose, fleshy, herbaceous or suffrutescent, densely branched annuals forming small, leafy mats; branches slender, from the top of a short, slender taproot. Branching alternate, sympodial (at least in part). Leaves small, opposite, entire, fleshy, the members of a pair distinctly unequal; blades elliptic to elliptic-oblong or ovate, apex acute or obtuse, base acute to rounded; petiole often as long as the blade, dilated below, the margins scarious, clasping, those of a leaf pair sometimes connate and sheathing the node; stipules scarious, laciniate. Flowers appearing axillary, solitary, small, accompanied in the axil by two small, scarious, laciniate bracteoles. Sepals 5, unequal, erect, united below for about one third their length, the margins scarious, the lobes thicker and slightly keeled above, lacking a dorsal appendage, green or purple-tinged without, white to reddish within, quincuncial, persistent. Stamens 1–5, alternate with and shorter than the calyx lobes, inserted at the sinuses, persistent; anthers small, subglobose, whitish; filaments filiform. Styles 2[–3], very short, erect, slightly united below; ovary

superior, 2[–3]-loculate at anthesis; ovules numerous, campylotropous, exarillate; placentation axile. Fruit a subglobose, 1-loculate, thin-walled pyxis circumscissile below the middle, remnants of the septum remaining; seeds numerous, small, on long funiculi from the persistent central axis, subreniform. Seed coat smooth, brown; embryo arcuate around a scanty, starchy endosperm; cotyledons fleshy. (Including *Radiana* Raf., *Millegrana* Juss. ex Turpin.) TYPE SPECIES: *C. humifusa* Turpin. (Name from Greek, *kypsele*, a hollow vessel or a beehive, probably because of the shape of the pyxis.)

A very small New World genus of possibly three species, inhabiting drying swamp land and other moist, disturbed sites on shore lines, hammocks, and sandy pinelands. The genus is represented in our area by *Cypselea humifusa* in peninsular Florida and in Louisiana; this species is also known from central California. It may have been introduced into all three of these areas from the West Indies (Cuba, Hispaniola, St. Thomas, Guadeloupe, and others).

*Cypselea humifusa*, usually with green calyx lobes and with stamens mostly one to three, was first described from Haiti (Saint Domingue). *Cypselea rubriflora* Urb., with longer pedicels, reddish calyx lobes and five stamens, has been described from Cuba. *C. Meziana* K. Müll., of Paraguay, is said to differ from both of these species in having three styles and a three-loculate ovary.

The extent and taxonomic significance of color variation in the calyx lobes and other plant parts is not known, since collectors' notes on color are rare. Specimens of a recent collection by Thieret of *Cypselea humifusa* from St. Landry Parish, Louisiana, are lightly tinged with purple in the stems, leaf tips, calyx tube and lobes, and darkly so in the fruits, but such coloration is lost in older herbarium specimens, which become rather brown.

Although plants of the genus are glabrous, the nodes often appear pilose due to the protruding segments of the laciniate bracteoles and stipules. The solitary flowers appear to be axillary but are actually terminal. Growth of the vegetative axis beyond each flower is sympodial, the axillary bud of the larger leaf continuing the axial growth while the axillary bud of the smaller leaf produces only a short fascicle of small leaves. At anthesis the ovary is distinctly septate, with axile placentation, but the septum is ruptured during fruit development, giving the appearance of being unilocular with the free-central placentation that is so often cited in taxonomic accounts. Anomalous secondary thickening and solitary crystals are reported for the genus. Chromosome counts are lacking, and the identity of the red pigments is not known.

The genus is considered to be closely related to *Sesuvium* L. and *Trianthema* L. (Müller).

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Subfamily TETRAGONIOIDEAE Lindl.

5. **Tetragonia** Linnaeus, Sp. Pl. 1: 480. 1753; Gen. Pl. ed. 5. 215. 1754.

Annual or perennial herbs or subshrubs with somewhat succulent, densely papillate [or pubescent], procumbent or ascending, spreading branches. Leaves cauline, mostly alternate, petiolate, exstipulate; blades entire, fleshy, ovate-deltoid to ovate-rhomboid, the apex acute to obtuse, the base mostly truncate to cuneate, papillate [or pubescent]. Flowers axillary [or terminal], solitary or paired [or few in a cymose or spike-like cluster], nearly sessile or short pedicellate, perfect [or polygamous through reduction of the ovary]. Sepals 4 (3–5), fleshy, united in a tube and adnate to the ovary, color varying in ours from greenish to yellowish within [to reddish]. Stamens 7–13 [1 to many, or in fascicles alternate with the calyx lobes], inserted on the floral tube, shorter than the calyx lobes;

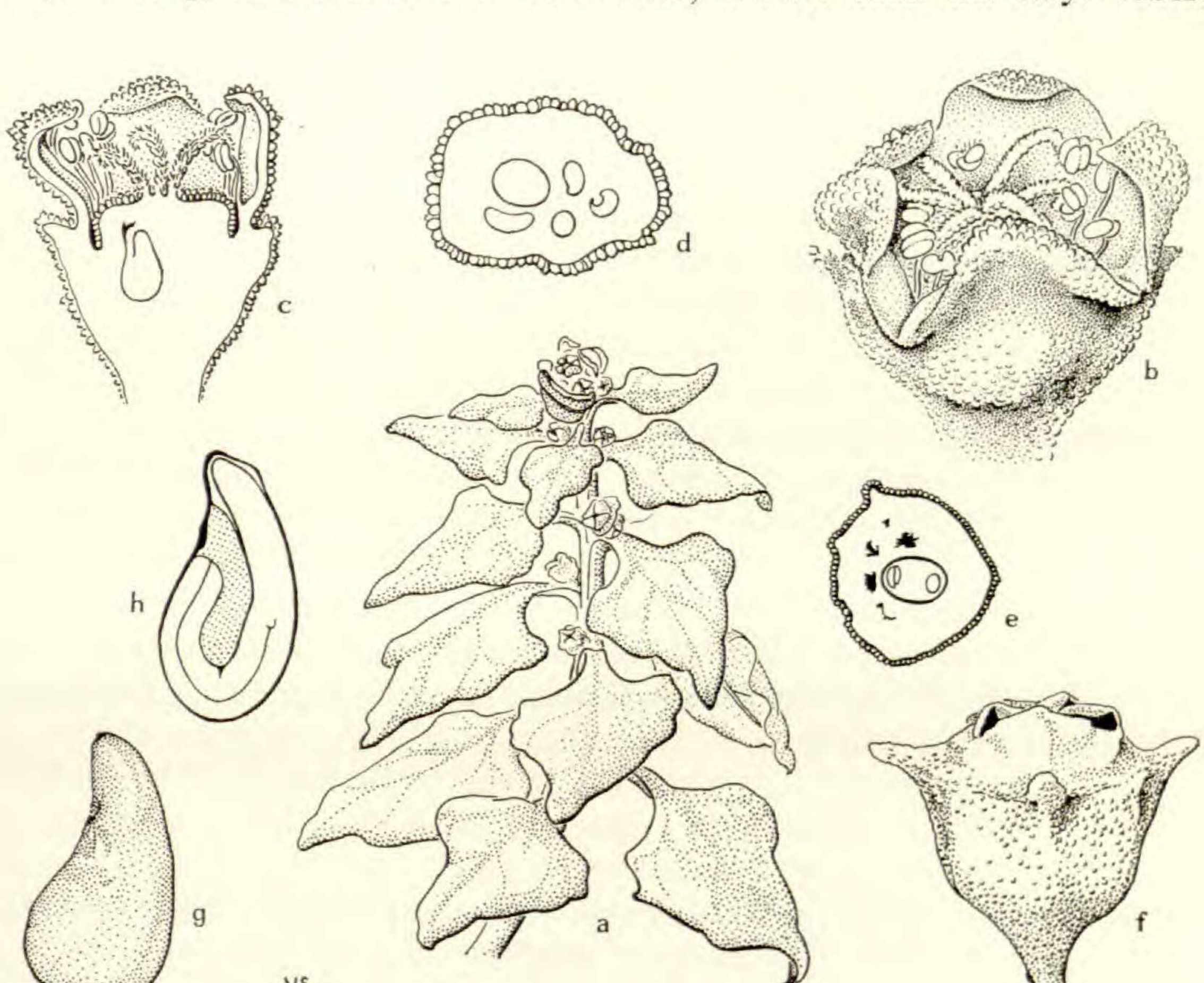


FIGURE 4. **Tetragonia.** a–h, *T. expansa*: a, flowering branch, × ¾; b, flower, × 8; c, flower in semidiagrammatic vertical section to show perigynous floral organs — note solitary pendent ovule in one locule, × 6; d, cross section of ovary showing unequal growth of fertile and sterile carpels, × 8; e, cross section of a fruit – note seed of single fertile carpel, sterile locules crowded out, × 4; f. indehiscent horned fruit, × 3; g, seed, × 10; h, seed in section, to show curved embryo partly inclosing endosperm (stippled), × 12.

anthers subglobose; pollen yellow. Carpels 3–9 [rarely 1 or 2], united; styles 3 or more, equaling the locules, short, erect; ovary half-inferior [to inferior], 3–9-loculate; placentation axile; ovules solitary, pendent, campylotropous (?). Fruit obconic, nutlike, bony, indehiscent, with usually 4 or 5 short, sharp horns [or fruit compound, variously angled to winged or thorny, the thorns often producing axillary buds or sessile flowers in *T. dimorphantha* Pax!]. Seeds solitary, ± pyriform to subreniform; seed coat smooth, membranaceous, light brown; embryo hook or horse-shoe shaped [to arcuate] around an abundant, white, starchy endosperm; cotyledons linear-oblong, fleshy. (Including *Demidovia* Pall.) LECTOTYPE SPECIES: *T. fruticosa* L.; see Hitchcock & Green, Int. Bot. Congr. Cambridge, 1930. Nomencl. Prop. Brit. Bot. 159. 1929. (Name from Greek *tetra*, four, and *gonia*, angle, in reference to the fruit; a shortened form of the pre-Linnaean name *Tetragonocarpos*.) — NEW ZEALAND SPINACH.

A genus of about 50–75 species distributed chiefly in the Southern Hemisphere. More than half the species are restricted to southern Africa, while a large number are concentrated in southern South America, particularly in Chile. A few species occur in Australia, New Zealand, Polynesia, southeastern Asia, and North Africa. The genus is represented in our area by *Tetragonia expansa* Murr. (*T. tetragonoides* (Pall.) O. Kuntze), $2n = 32$, of subgenus TETRAGONOIDES. Although native to the coastal regions of the southern and western Pacific, *T. expansa* has been widely cultivated as a leafy vegetable and has become naturalized in many areas after escaping from cultivation. The species is reported from old fields and waste places in North Carolina and Florida, Bermuda, Connecticut and Massachusetts, and California. The number of specimens available is small, however, and it is not clear whether the species is truly naturalized in these areas or occurs only as a waif after escaping cultivation. None of the available specimens is complete; the lower parts are missing from all of them. The broad distribution of *T. expansa* around the shores of the Pacific basin is probably explained by Hashima's finding that the fruits can stay afloat in sea water for more than a month, with the enclosed seeds retaining their viability, thus allowing for long-distance dispersal by ocean currents.

From other genera of Aizoaceae *Tetragonia* is distinguished by its half-inferior to inferior ovaries with a single pendent ovule in each locule, by the absence of staminodial bodies (Adamson), and by its indehiscent, cartilaginous or stony (and sometimes compound) fruits. The genus has been subdivided into two or three sections (Pax & Hoffmann, Post & Kuntze), or two or four subgenera (Fenzl, Adamson). The most recent revision is that of Adamson who recognizes four subgenera: TETRAGONIA (containing seven series), TETRAGONOIDES (DC.) Adamson, ANISOSTIGMA (Schinz) Adamson, and TRIBULOCARPUS (Moore) Adamson. Only subgenus TETRAGONOIDES ranges beyond southern Africa.

The systematic position and relationships of *Tetragonia* are not clear. The genus was once considered close to *Mesembryanthemum* (Baillon,

Bentham & Hooker, De Candolle, Pax) on the basis of floral structure (presence of a floral tube, numerous stamens, half-inferior to inferior ovaries), but more often it has been segregated as the type, if not the sole member, of a tribe Tetragonieae (Fenzl, Müller, Pax & Hoffmann), subfamily Tetragonioideae (Eckardt, Schwantes), or family Tetragoniaceae (Friedrich, Lindley, Nakai).

The chromosome complement of the genus is based on eight, with numbers of $2n = 32$ reported for *Tetragonia expansa*, *T. crystallina* L'Hérit., and *T. echinata* Ait., and $2n = 96$ for *T. trigyna* Banks & Sol. ex Hook. f.

Payer described and illustrated the floral organogeny of *Tetragonia expansa* in detail, but the morphology and anatomy of the genus have received little attention. Secondary thickening in stems and roots is anomalous, producing xylem and phloem in more or less complete concentric rings. Large bladder-like water-storage cells occur in the epidermis among smaller unspecialized cells. In dried specimens these become collapsed and flattened, giving the plant a hoary appearance. Stomata of the ranunculaceous type are reported. Columnar crystals occur in the pith of *T. spicata* L. f., and clustered crystals in the cortex of *T. expansa*.

Apart from a statement of D'Hubert on the presence of starch grains in the embryo sac of the "Tetragoniées" the embryology of the genus is apparently unknown. Coutinho *et al.* investigated the structure of chloroplasts in *T. expansa* and found them intermediate in form between the Euglena and Aspidistra types, in that they contain few, small, irregular grana and a relatively large amount of stroma lamellae extending throughout the length of the chloroplast.

Red pigments of the betacyanin type are reported in *Tetragonia crystallina*. Toxic alkaloids and saponins are also reported for *T. expansa* (as *T. tetragonoides*).

The economic significance of *Tetragonia expansa* appears to rest solely on its cultivation as a leafy vegetable, a substitute for spinach. Analysis of the dried plant, however, has shown that the content of anhydrous oxalic acid may attain levels of 10 per cent or greater, thus posing the danger of sharply reducing the absorption of calcium from a diet containing adequate amounts of that element.

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ARNOLD ARBORETUM
HARVARD UNIVERSITY

Present address:
DEPARTMENT OF BOTANY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NEW HAMPSHIRE 03857

# SEEDLING MORPHOLOGY IN THE JUGLANDACEAE, THE COTYLEDONARY NODE

LOUIS F. CONDE AND DONALD E. STONE [1]

DESPITE NUMEROUS STUDIES in the Juglandaceae, the number of genera and their phylogenetic positions are still unsettled. *Alfaroa*, *Annamocarya*, *Carya*, *Engelhardia*, *Juglans*, *Oreomunnea*, *Platycarya* and *Pterocarya* were recognized by Leroy (1955), while Manning (Manning & Hjelmqvist, 1951; Manning, 1961) has continued to emphasize the similarities of *Oreomunnea* (*Engelhardia* sect. OREOMUNNEA sensu Manning) with *Engelhardia* and those of *Annamocarya* (*Carya* sect. RHAMPHOCARYA sensu Manning) with *Carya*, thus arguing for six genera. The walnut family is generally conceded to be a very natural assemblage (Lawrence, 1951; Cronquist, 1968), so it is not surprising that generic boundaries are debatable. This is not to say that the taxa are difficult to characterize; all representatives are, in fact, large forest trees which may be recognized by combinations of features that range from differences in bark and wood (Heimsch & Wetmore, 1939) to phyllotaxy (Standley, 1927), flowers (Manning, 1940, 1948), pollen (Whitehead, 1965), inflorescences (Manning, 1938), and particularly fruits (Leroy, 1955). It is precisely this comparative wealth of information that makes the Juglandaceae so tempting to the phylogenist.

Because of the remarkable diversity of the flowers and fruits and as a result of some preliminary studies on seedling germination, we had reason to believe that seedling morphology would be useful in assessing generic relationships. An earlier study by Davey (1916) on the Amentiferae covered the descriptive aspects of two species of *Carya*, four species of *Juglans*, one of *Pterocarya*, and the monotypic genus *Platycarya*. A wide variety of cotyledonary nodal types is reported in the literature. Trilacunar and multilacunar nodes are noted for *Carya* (Davey, 1916; Langdon, 1934), and *Juglans* (Davey, 1916, 1935; Nast, 1941; Gravis, 1943) and unilacunar two-trace nodes for *Platycarya* and *Pterocarya* (Davey, 1916). This diversity of nodal types, representing both the most primitive and advanced forms as proposed by Marsden and Bailey (1955) in their study of nodal evolution, as well as the absence of information on the primitive members of the family, namely *Alfaroa* and *Engelhardia*, offered additional promise for the current survey. An implicit consideration of our study was an examination of the evidence giving rise to the general belief

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